Litter mass-loss rates and decomposition patterns in some needle and leaf litter types. Long-term decomposition in a Scots pine forest. VII

BJÖRN BERG[1]
Department of Ecology and Environmental Research, P.O. Box 7072, Swedish University of Agricultural Sciences, S-750 07 Uppsala, Sweden

AND

GUNNAR EKBOHM
Department of Statistics, Swedish University of Agricultural Sciences, S-750 07 Uppsala, Sweden

Received July 7, 1990

BERG, B., and EKBOHM, G. 1991. Litter mass-loss rates and decomposition patterns in some needle and leaf litter types. Long-term decomposition in a Scots pine forest. VII. Can. J. Bot. **69**: 1449–1456.

The decomposition dynamics of four types of needle litter and three types of leaf litter were followed for 4 years. Mass losses and certain chemical changes were studied. Most of the nutrient-rich litters appeared to decompose relatively quickly during the first 12–18 months. After 3–4 years, however, their accumulated mass losses were lower compared with litter types that intially had lower rates. Thus the more nutrient-rich litters had considerably lower mass-loss rates in the later stages. This pattern was even more pronouced for extract-free lignocellulose: its mass-loss rate was negatively related to the lignin concentration, which increased progressively as litter decomposition proceeded. During late stages in litter with a high nitrogen content, there was also a clear negative relation between nitrogen concentration and lignin mass-loss rate, as well as between nitrogen concentration and litter mass-loss rate. By extrapolation of measured mass-loss values, maximum values for accumulated litter–mass loss were estimated. A nonlinear statistical model predicted that the proportion of mass lost through decomposition should be 50% for grey alder leaves, 54% for green leaves of white birch, and 57% for brown leaves of white birch. For Scots pine the predicted maximums for accumulated mass loss were 68% for green needles and 89% for brown needles, whereas corresponding values for lodgepole pine needles were 81% (green) and 100% (brown). Lodgepole pine is an introduced species in this system.

Key words: litter, decomposition, lignin, nitrogen, maxium mass loss.

BERG, B., et EKBOHM, G. 1991. Litter mass-loss rates and decomposition patterns in some needle and leaf litter types. Long-term decomposition in a Scots pine forest. VII. Can. J. Bot. **69** : 1449–1456.

Les auteurs ont suivi pendant 4 ans la dynamique de la décomposition de quatre types de litière d'aiguilles et trois types de litière de feuilles. Ils ont étudié les changements de perte en masse et en certains composés chimiques. La plupart des litières riches en nutriments semblent se décomposer relativement rapidement au cours des 12–18 premiers mois. Après 3–4 ans, cependant, les pertes en masse cumulative sont plus faibles comparativement aux types de litière qui montrent des taux plus faibles au départ. Ainsi les litières plus riches en nutriments ont des taux de perte en masse plus faibles aux stades les plus avancés. Ce patron est encore plus prononcé pour la ligno-cellulose sans extractibles: son taux de perte en masse montre une relation négative avec la concentration en lignine, laquelle augmente progressivement à mesure que la décomposition de la litière évolue. Au cours des derniers stades, chez les litières à forte teneur en azote, il y a également une relation négative nette entre la concentration en azote et le taux de perte en masse de la lignine aussi bien qu'entre la concentration d'azote et le taux de perte en masse de la litière. Les auteurs ont estimé la valeur maximale de la perte en masse de litière cumulative, en extrapolant les valeurs des pertes en masse mesurées. Un modèle statistique non-linéaire permet de prédire que la proportion de la masse perdue par décomposition devrait être de 50% pour les feuilles de l'*Alnus incana*, de 54% pour les feuilles vertes de *Betula pubescens* et de 57% pour les feuilles brunies de *B. pubescens*. Pour le *Pinus sylvestris* les valeurs maxima prédites pour les pertes en masse cumulées sont de 68% pour les aiguilles vertes et 89% pour les aiguilles brunies, alors que les valeurs correspondantes pour les aiguilles de pin lodgepole sont de 81% (vertes) et 100% (brunes). Le pin lodgepole est une espèce introduite dans ce système.

Mots clés : litière, décomposition, lignine, azote, perte en masse maximum.

[Traduit par la rédaction]

Introduction

Plant litter in boreal coniferous forests is decomposed mainly though microbial activity. The quantitative contribution of soil animals to decomposition is considered to be minimal (Persson et al. 1980). Thus the environmental factors most important in regulating the turnover rate of litter tend to be those that regulate the activity of microorganisms, i.e., soil temperature, soil moisture content, nutrient availability, energy-source availability.

In addition to climate, the litter's chemical composition strongly regulates mass-loss rates (McClaugherty and Berg 1987). Total concentrations of certain nutrients, such as nitrogen and phosphorus, in litter have been proposed as rate-enhancing factors (Melin 1930; Millar et al. 1948), whereas lignin has been suggested as a rate-retarding compound (Fogel and Cromack 1977). Berg and Staaf (1980) proposed a two-phase model for describing the decomposition dynamics of Scots pine needle litter.

---

[1] Present address: Department of Forest Soils, P.O. Box 7001, Swedish University of Agricultural Sciences, S-750 07 Uppsala, Sweden.

Printed in Canada / Imprimé au Canada

In some cases an initially high decomposition rate can decrease so strongly that after only a few months the mass-loss rate is almost too low to be measured (Berg et al. 1982*a*; Berg and Wessen 1984). In their studies on litter decomposition rates in an experimental, animal-free environment, Howard and Howard (1974) found that mass-loss rates decreased so fast that they could estimate final limits for accumulated mass loss in their different litter types. These limits were estimated as asymptotic values towards which the decomposition proceeded. Such asymptotic values reflecting a maximum decomposition would mean that an accumulation of organic matter would take place at a rate dependent on the value of the asymptote, i.e., how much of the litter that was decomposed.

Lignin can have a regulating effect on litter mass-loss rates during late stages of decomposition. Berg et al. (1982*a*) and Berg and Wessen (1984) reported that the lignin mass-loss rate was lower in nitrogen-rich litters than in nitrogen-poor ones. Two types of observations help to explain the nitrogen-related difference in mass-loss rates for the sulfuric acid lignin fraction: (*i*) amino acids and amonium ions can repress the formation of lignolytic enzymes in various fungal species (Keyser et al. 1978; P. Ander, personal communication and (*ii*) degradation products of lignin may react with ammonia or amino acids to form recalcitrant complexes (Bremner and Shaw 1957). Laboratory experiments suggest that the concentration of ammonium–ammonia could be limiting for this kind of reaction (Axelsson and Berg 1988). This topic has been reviewed by Nömmik and Vahtras (1982).

This study has two aims: (*i*) to test an hypothesis that lignin and nitrogen act as rate-retarding factors during the late stages of litter decomposition (Berg and Staaf 1980; Berg et al. 1987) and (*ii*) to verify, in a field study, the conclusions of Howard and Howard (1974) that there are maximum values for accumulated litter mass loss.

Site description

The site used in this study was a Scots pine stand about 130 years old of the former Swedish Coniferous Forest Project research site, Ivantjärnsheden, central Sweden (60°49′N, 16°30′E) at an altitude of 185 m asl on a flat area of deep glacifluvial sand sediments. The mean annual precipitation at a nearby village is 609 mm (1931–1960) and the mean annual temperature is +3.8°C. The length of the growing season is about 160 days (number of days with a daily temperature higher than 6°C, Axelsson and Bråkenhielm 1980). The forest has been described in earlier papers (e.g., Berg et al. 1982, 1984).

The soil profile is an orthic humoferric podzol (iron podzol) with a weakly developed A horizon (bleached horizon; 2–7 cm) and a typical mor humus. A very loose L horizon (A_{00}), interwoven with living mosses and lichens, covers an F–H horizon (A_{01}–A_{02}) of 5–10 cm. The F horizon (A_{01}) and the H horizon are almost indistinguishable from each other. The pH range is 3.9–4.2 in the F–H horizon and 4.6–4.8 in the upper mineral soil. The parent mineral material as well as the whole soil is considered to be very poor in essential nutrients. The C:N ratio of the F–H horizon (A_{01}–A_{02}) is 42.3.

Materials and methods

Needle litter collection, storing, weighing, field incubations, and sampling of litter bags

Scots pine needle litter was sampled at Ivantjärnsheden in the autumn of 1982 from the branches of trees in a stand that was about 15 years old. Brown needles from the needle generation to be shed were taken at abscission from trees growing in an area of about 20 × 50 m^2 and were stored at −20°C until sample preparation. Green needles were sampled from the same area and taken from the second and third needle generations. Brown leaves of white birch were sampled at the same site and time as Scots pine needles. Green leaves of white birch (*Betula pubescens*) and grey alder (*Alnus incana*) were sampled at the same site in early August. Brown needle litter and green needles from lodgepole pine (*Pinus contorta*) were sampled from trees about 25 years old at a research site close to the town of Malung, central Sweden (cf. Berg and Lundmark 1987).

Before weighing, the needles and leaves were air dried at room temperature to about 5–8% moisture. Dry mass was determied on 25 samples at 85°C, and the largest difference in moisture content was less than ±0.5% units of the average.

Litter bags (8 × 8 cm^2) were made of terylene net with a mesh size of about 1 mm. Each type of litter was put in separate litter bags, and 0.6–1.0 g of needle litter was enclosed in each bag. The bags were placed on the litter (L) layer in a measurement plot (1 × 1 m^2) in each of 25 plots in a randomized design in the plot measuring 2 ha. They were fastened to the ground by 10–15 cm long metal pegs. The incubations were made in October 1982. Samplings took place three to four times annually. On each sampling occasion we collected one sample of each litter type from each of the 25 spots. The litter bags were transported directly to the laboratory for processing, and 20 of the samples were taken for mass-loss determination and 5 for determination of fungal biomass (Berg 1991).

Determination of mass loss

The 20 samples of each type were stored in a deep freeze. Plant remains, such as mosses, lichens, and cowberry, were removed and the loss of dry mass was determined after drying the samples to a constant mass at 85°C. Mean values of mass loss were calculated for each sampling. After this the samples were combined for chemical analyses.

Chemical analyses

The combined samples were ground in a laboratory mill equipped with a 1-mm screen. The amounts of water-soluble and ethanol-soluble substances were determined by sonicating the milled samples three times in a sonicator bath and weighing the samples after filtration and drying. The analyses for sulfuric acid lignin and solid carbohydrates (xylan, mannan, galactan, rhamnan, araban, and glucans) in the needle samples were carried out according to Bethge et al. (1971) (see also Berg et al. 1982*b*).

The analyses for mineral nutrients were carried out as described by Staaf and Berg (1982).

A statistical model for decomposition

Decomposition of some litter types approaches a maximum level. Howard and Howard (1974), who compared several statistical models for such a case, preferred an asymptotic, nonlinear model with three parameters, *A*, *B*, and *r*. Since, by definition, the sum of *A* and *B* is equal to 100%, there are, in fact, only two free parameters (i.e., $A = 1 - B$). A slight reparameterization ($m = B$ and $k = -B \ln r$) resulted in the following nonlinear model, which we found to be more feasible to use:

$$[1] \quad ml = m(1 - e^{-kt/m})$$

where *ml* is the accumulated mass loss (%) and *t* is time in days. The parameter *m* represents the maximum accumulated mass loss (asymptotic level) and the parameter *k* is the initial decomposition rate. The basis for our choice of the above expression was that we regarded the substrates as consisting of a nondegradeable component and one decomposing exponentially.

Terminology

Our lignin analyses are based on the sulfuric acid lignin method, which does not discriminate between lignin and other compounds such as humic acids (cf. Berg and Theander 1984). Thus, the word "lig-

TABLE 1. Initial composition of organic-chemical components and nutrients in seven litter types used in the decomposition experiment

	Concn. of component (mg g^{-1})			Relative proportions of components[a] (mg g^{-1})					
	Substances soluble in:								
	Water	Ethanol	Lignin	Rhamnan	Xylan	Galactan	Mannan	Araban	Glucans
White birch leaves									
Brown	241	57	330	16	77	44	14	49	166
Green	222	57	322	12	54	51	9	36	168
Scots pine needles									
Brown	164	113	231	3	23	32	75	36	245
Green	180	90	220	2	19	30	75	23	217
Lodgepole pine needles									
Brown	103	42	381	6	34	46	90	48	254
Green	147	36	346	33	29	37	81	40	239
Grey alder leaves	254	39	264	9	30	32	10	44	116

	Concn. of component (mg g^{-1})						
	N	P	S	K	Ca	Mg	Mn
White birch leaves							
Brown	7.7	1.05	0.80	4.66	11.80	3.30	1.23
Green	17.4	1.80	1.32	6.95	5.56	1.99	0.36
Scots pine needles							
Brown	4.8	0.33	0.55	1.07	4.42	0.49	0.79
Green	15.1	1.31	1.13	4.67	2.77	0.82	0.26
Lodgepole pine needles							
Brown	3.9	0.34	0.62	0.56	6.35	0.95	1.79
Green	10.5	0.82	1.17	3.84	3.99	0.93	0.82
Grey alder leaves	30.7	1.37	6.12	15.6	12.3	2.32	0.10

[a] Calculated to be 100% together with lignin and solubles.

nin" is fully correct only in the very early decomposition stages. Nevertheless, in an investigation using high-resolution ^{13}C NMR, Norden and Berg (1989) did not find any differences in the patterns of the aromatic peaks between litter samples collected at different stages of decomposition (0 and 70% accumulated mass loss). This should partly justify the use of the word lignin. Thus the term has been used here for the sake of simplicity, even though it is not fully correct. "Holocellulose" refers to cellulose plus hemicelluloses, and the term "lignocellulose" refers to holocellulose plus lignin.

Data set

The complete data set for this study may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council of Canada, Ottawa, Ont., Canada K1A 0S2, and will, in addition, be published elsewhere (Berg et al. 1991).

Results and discussion

Chemical composition of the litter types

The litter types in this study showed a relatively wide range in chemical composition (Table 1). Water-soluble substances ranged from 100 mg g^{-1} in lodgepole pine needles to 250 mg g^{-1} in leaves of grey alder and white birch. Ethanol-soluble compounds, including phenolics among other substances, were present at low concentrations in grey alder leaves and at fairly high concentrations in Scots pine needles. Scots pine needles had low concentrations of lignin, whereas leaves of white birch and needles of lodgepole pine had high concentrations, i.e., 320–330 and 350–380 mg g^{-1}, respectively. In terms of polymer carbohydrates, grey alder leaves had a low concentration of glucans (about 120 mg g^{-1}) compared with relatively high concentrations in lodgepole pine needles (240–250 mg g^{-1}). White birch leaves had higher concentrations of xylans than the other litters, and all species had low concentrations of rhamnans.

The range in nutrient composition was also large. Nitrogen concentrations ranged from 31 mg g^{-1} in alder leaves to about 4 mg g^{-1} in brown lodgepole pine needles. The brown leaves of birch were richer in both nitrogen (7.7 mg g^{-1}) and phosphorous (1 mg g^{-1}) than the brown needles of both pine species (4–5 and around 0.33 mg g^{-1}, respectively). Although grey alder leaves had high concentrations of phosphorus (1.4 mg g^{-1}), the green leaves of birch and green needles of both pine species had even higher phosphorus concentrations. Alder leaves were also rich in potassium (15.6 mg g^{-1}) and calcium (12.3 mg g^{-1}). Brown leaves of white birch also had a high concentration of calcium (11.8 mg g^{-1}), whereas levels in the other litters were below 6 mg g^{-1}. Relative differences in magnesium concentrations between litter types were similar to those described for calcium, whereas manganese concentrations were high in green needles of lodgepole pine and in brown leaves of white birch (1.2–1.8 mg g^{-1}). Alder leaves and green leaves of white birch and Scots pine, on the other hand, had fairly low concentrations of this element.

Litter mass loss

Initially, mass-loss rates were higher for leaves and green needles than for brown needle litters (Fig. 1*a*). However, after about a year, litter types with high initial mass-loss rates began decomposing more slowly, and after about 4 years in the field they had the lowest accumulated mass losses (Fig. 1*a*). These

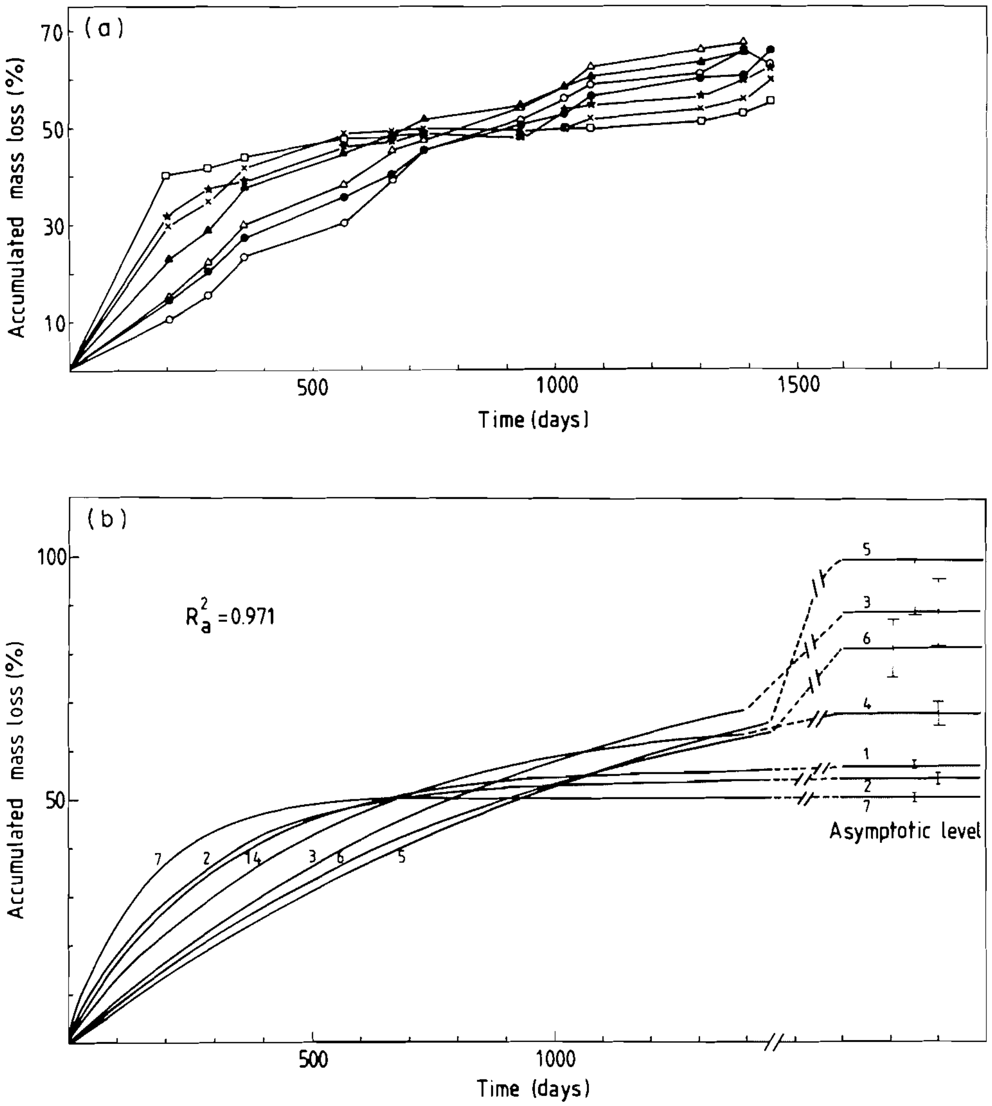

FIG. 1. Accumulated mass loss for seven litter types incubated in a 130-year-old Scots pine forest. △, brown Scots pine needle litter; ▲, green Scots pine needles; ○, brown lodgepole pine needle litter; ●, green lodgepole pine needles; ×, brown leaves of white birch; ★, green leaves of white birch; □, grey alder leaves. (*a*) Litter mass. (*b*) Estimated initial litter mass-loss rates and asymptotic values for accumulated mass loss. 1, white birch, brown leaves; 2, white birch, green leaves; 3, Scots pine, brown needles; 4, Scots pine, green needles; 5, lodgepole pine, brown needles; 6, lodgepole pine, green needles; 7, grey alder leaves. Vertical bars denote SE.

results support the finding by Berg et al. (1982*a*) that more nutrient-rich and initially quick decomposing green Scots pine needles decomposed more slowly than brown needles during later stages of decomposition. Berg and Wessén (1984) noted a similar phenomenon when comparing mass-loss rates for brown needles of Scots pine and leaves of white birch. In the present study this effect was more pronounced, especially with regard to the mass-loss patterns of the extract-free lignocellulose of the seven litter types.

The decomposition patterns of the seven litter types are illustrated in Fig. 1; Fig. 1*b* shows the fitted nonlinear model (model 1). For estimating the parameters of model 1 we used the NLIN program of SAS Institute Inc. (1979). For estimating and comparing the parameters for all seven litter types, the dummy-variable technique was utilized. Since 14 parameters were simultaneously estimated using 82 observations (see Table 2), the residual variance was estimated with 68 degrees of freedom.

The results (Table 2) indicated that the final levels of accumulated mass loss ($\hat{m}$) resulting from decomposition should differ between litters. Thus, for alder leaves, the estimated maximum mass loss should be 51%, whereas for white birch leaves (both green and brown) the final level should be approximately the same (54–56%, not significantly different). Estimated maximum levels for Scots pine needles were 68% (green) and 89% (brown). Like green Scots pine needles, green needles of lodgepole pine had a lower asymptote (81%) than brown needles, which reached a value of 100% and thus cannot be considered to have an asymptote. The mass-loss patterns of the green and brown lodgepole pine needles were not significantly different from each other. When the whole system was analyzed, i.e., all curves were fitted simultaneously, a high adjusted R^2 value of 0.971 was obtained, indicating a reasonably good fit.

A clearly significant negative linear relation was found between the maximum mass losses (asymptotes) estimated ($\hat{m}$)

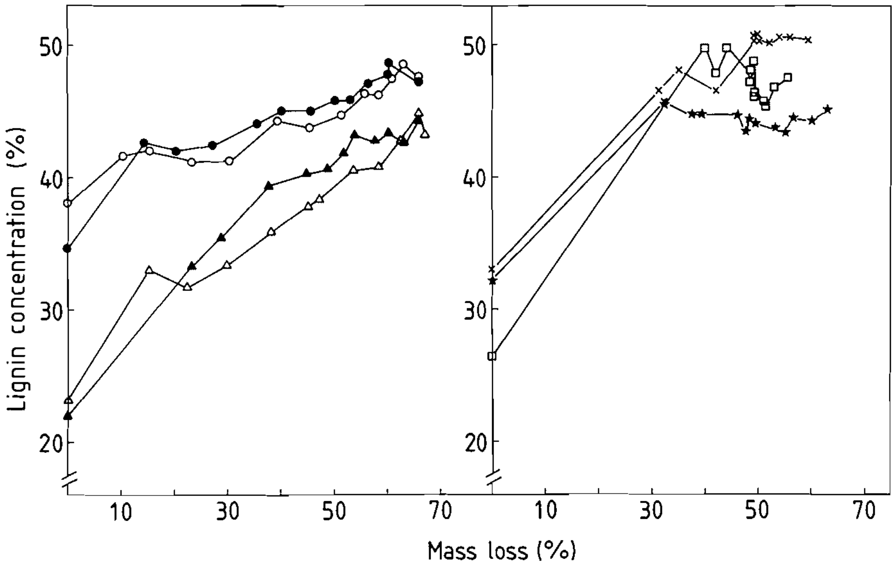

FIG. 2. Concentration of lignin in seven litter types in relation to litter mass loss. Symbols as in Fig. 1.

TABLE 2. Estimated initial decomposition rates and estimated asymptotic values for accumulated mass loss

	Initial rate (‰ day^{-1})	Asymptotic value (%)	n
White birch leaves			
Brown	0.187(0.013)	56.9 (1.3)	12
Green	0.206(0.015)	54.3 (1.1)	12
Scots pine needles			
Brown	0.093(0.006)	89.0 (7.0)	11
Green	0.136(0.008)	68.0 (2.5)	11
Lodgepole pine needles			
Brown	0.075(0.005)	100.0 (11.1)	12
Green	0.086(0.005)	81.5 (6.0)	12
Grey alder leaves	0.336(0.035)	50.6 (0.9)	12

NOTE: Standard error is given in parentheses. The seven litter types were incubated in a 130-year-old Scots pine forest. total number of observations was 82.

TABLE 3. Relations between the estimated parameter in [1], k (initial decomposition rate), and initial concentration of nitrogen, phosphorus, sulfur, and water-soluble substances

(A) Correlation matrix

	N	P	S	Water solubles
k	0.893**	0.691	0.869*	0.879**
Nitrogen		0.733	0.908**	0.686
Phosphorus			0.414	0.735
Sulfur				0.580

(B) Adjusted coefficients for determination (R_a^2) obtained in simple and multiple linear regressions

k = f(N)	0.757
k = f(P)	0.373
k = f(S)	0.705
k = f(water solubles)	0.726
k = f(N, water solubles)	0.897
k = f(S, water solubles)	0.949
k = f(N,P,S, water solubles)	0.952

*$p < 0.05$.
** $0.05 < p < 0.01$.

and two initially rate-promoting parameters, i.e., concentrations of phosphorous and concentrations of water solubles. Although not significant, the correlation between maximum mass loss and the nitrogen concentration obtained a relatively high r value (-0.754; $n = 7$; $p < 0.1$) (Table 4). These asymptotic values were obtained in a field study where soil animals had free access to the litter. Our system was however, very nutrient poor and had low numbers of soil animals. In fact, Persson et al. (1980) estimated that more than 95% of the decomposition was carried out by microorganisms.

Howard and Howard (1974) estimated asymptotic values for deciduous leaf litters that were incubated in experimental field systems free from soil animals. Although their system and litters were quite different from ours, some limited comparisons can be made, especially since the same mathematical relationship was used. The range over which their leaf litters reached asymptotic decomposition values was similar to that found here, namely 36–65% accumulated mass loss. Furthermore, the asymptotes of their leaf litters and ours were in the same region and well below that of the needles. When the asymptote values obtained by Howard and Howard (1974) were related to the initial concentrations of nitrogen in their leaf litters, a clearly significant relation was found ($r = -0.823$; $p < 0.05$; $n = 7$). Thus for both systems there were negative relations between the level of the asymptote and factors promoting initial decomposition rates. The fact that this empirical relationship was found in two separate studies leads us to speculate that an initially high decomposition rate in the early stages favours the formation of low-molecular nitrogen compounds that can react with reactive groups in lignin and lignin remains (Nömmik and Vahtras 1982), creating a layer of compounds that microorganisms cannot degrade.

All these data were calculated for systems that were either free from soil animals or had a soil fauna with a low capacity to decompose litter, at least in the early decomposition stages. It is thus possible that the asymptotes reflect the point at which microbial decomposition came to a halt and other agents, such as soil animals, were needed for the process to continue. It is thus possible that nitrogen has a rate-retarding effect at this stage. Nitrogen may react with reactive lignin remains, form-

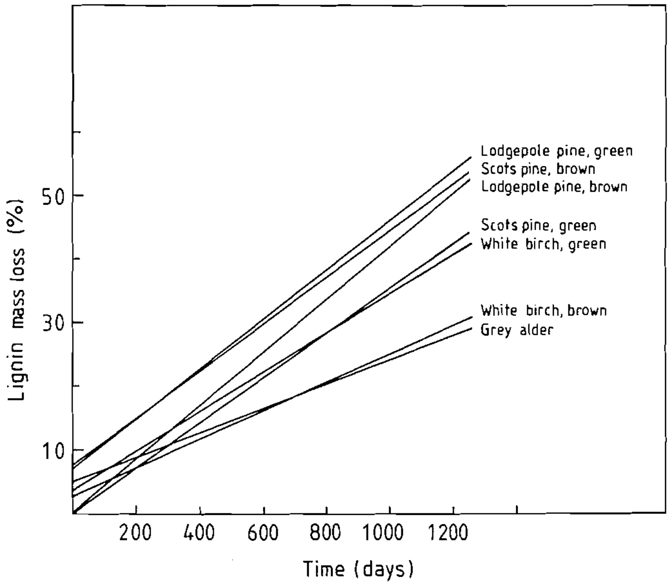

FIG. 3. Linear relations for decomposition of sulfuric-acid lignin vs. time in seven litter types incubated in a 130-year-old Scots pine forest (cf. Appendix, Table A1).

TABLE 4. Relations between the asymptotic value $\hat{m}$ and initial concentrations of nitrogen, phosphorus, sulfur, and water-soluble substances

(A) Correlations

	N	P	S	Water solubles
$\hat{m}$	−0.754	−0.891**	−0.560	−0.956***

(B) Adjusted coefficients for determination (R_a^2) obtained in simple and multiple linear regressions

$\hat{m}$ = f(N)	0.483
$\hat{m}$ = f(P)	0.752
$\hat{m}$ = f(S)	0.177
$\hat{m}$ = f(water solubles)	0.897
$\hat{m}$ = f(P, water solubles)	0.988

** $0.05 < p < 0.01$.
*** $0.01 < p < 0.001$.

ing a chemical barrier to the enzymes secreted by microorganisms (further discussed below), and mechanical breakdown by soil animals may be necessary to expose new surfaces susceptible to enzymatic attack.

Changes in chemical composition during decomposition

Concentrations of water-soluble substances decreased quickly (the 1st year) before reaching relatively similar and stable levels in all seven litter types. The ethanol-soluble fractions of the litters remained relatively constant, possibly indicating that their turnover rates were lower than those of the water-soluble fractions.

Concentrations of the recalcitrant sulfuric acid lignin fraction increased as decomposition proceeded, reaching relatively steady levels in the range of 45–51% (cf. Berg et al. 1984). For the pine needles these increases showed partially linear relations to accumulated mass loss (Fig. 2). For the leaf litters the increase occurred so quickly that the linear stage started and ended within the same sampling period, thus only the steady level could be seen.

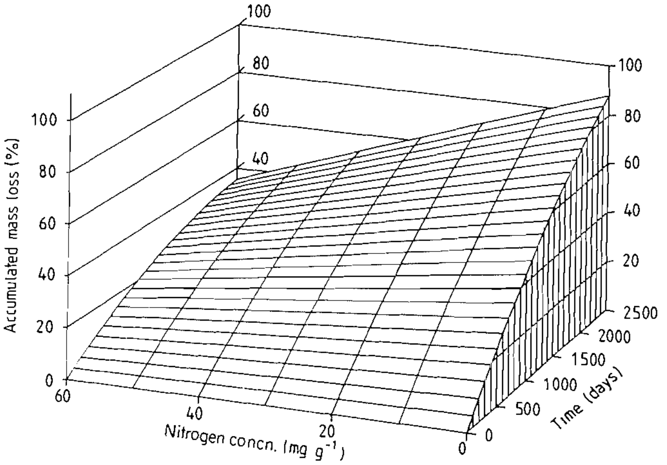

FIG. 4. Illustration of the negative relation between accumulated lignin mass loss changing with time (cf. Appendix, Table A1) and nitrogen concentration.

Rate-regulating factors

Significant linear relations were obtained between the two estimated parameters in model 1 and initial concentrations of nitrogen, phosphorus, sulfur, and water solubles (Table 3A). Thus the initial decomposition rate, k in [1], was related to initial concentrations of nitrogen, sulfur, and water-soluble substances. Note, however, that nitrogen and sulfur concentrations are strongly correlated, which complicates the interpretation of the causal relations. Because a multiple linear regression using initial concentrations of sulfur and water solubles gave an adjusted coefficient of determination (R_a^2) of 0.949, it seems reasonable to conclude that initial concentrations of nitrogen, sulfur, and water solubles largely determine the initial decomposition rate. Berg et al. (1987) found that for Scots pine needle litter the correlation with initial decomposition rate was stronger for phosphorus and sulfur than for nitrogen. For Norway spruce needle litter Berg and Tamm (1991) found that the water-soluble fraction had a significant influence on the decomposition rate, whereas nitrogen and phosphorus did not. Berg and Lundmark (1987), using a separate data set consisting of combined data from decomposition studies on Scots pine and lodgepole pine needle litter, found that water solubles and nitrogen had the strongest correlations with decomposition rates. Leaching of soluble material from the leaf litters should be limited (Bogatyrev et al. 1983), and no leaching from the needles should occur. Leaching can, of course, influence the rate of mass loss considerably, but since leaching from these kinds of litter was found to be low, we have assumed that a large part of the solubles was decomposed within the litter structure. Berg *et al.* (1987) found significant relations betwen rates of mass loss for Scots pine needle litter and initial concentrations of nitrogen, phosphorus, and sulfur, even when nutrient concentrations were much lower.

The mass-loss rate of needle litter of both Scots pine and lodgepole pine is retarded in proportion to lignin concentrations. This observation has been made repeatedly in the present Scots pine system and other pine ecosystems as well (Berg and Lundmark 1987; McClaugherty and Berg 1987).

Mass-loss rates of sulfuric acid lignin

The increase in accumulated mass loss over time for the lignin fraction of each litter type approximated a straight line

(Fig. 3). Brown lodgepole pine needle litter had the highest mass-loss (net loss) rate and grey alder leaves had the lowest (Fig. 3; cf. Appendix, Table A1). The estimates of mass-loss rates of lignin were based on the measured values for sulfuric acid lignin. Such an estimate of lignin decomposition rates may not seem to be entirely satisfying, as in some cases a net increase in the lignin fraction has been reported (Berg and McClaugherty 1988). Such an increase in sulfuric-acid lignin may be due in part to the chitin produced by certain ingrown fungal species and to the formation of humic acids (cf. Berg and Theander 1984). However, within a certain range of litter mass loss, there does not appear to be any extensive synthesis of entirely new products. Norden and Berg (1989) did not find any new peaks in the aromatic resonance region when applying high-resolution ^{13}C NMR to needle litter samples in decomposition stages from 0 to 70% accumulated mass loss. In addition, there was a clearly significant linear relation between the lignin concentrations estimated using ^{13}C NMR and sulfuric-acid lignin. If humic acids are synthesized, the measured process of lignin mass loss should be regarded as a net process.

As shown in Fig. 3 the lignin mass-loss rate was lowest for the nitrogen-rich litters and highest for the nitrogen-poor ones. Similar relations have been observed in earlier studies (Berg and Wessen 1984); Berg et al. 1982*a*), and we cannot exclude the possibility that nitrogen has a rate-retarding influence on the lignin decomposition process. Such an influence could be investigated by fitting a linear model including the nitrogen concentation of the litters. The estimated equation

$$[2] \quad ml = 45.4 \times 10^{-3}\,t - 0.0041 \times 10^{-3}\,t^2 - 0.35 \times 10^{-3}\,tN$$

in which t is time (in days) and N the nitrogen concentration (in mg g^{-1}) gave a reasonably good fit, with an adjusted coefficient of determination (R_a^2) of 0.677. Lignin mass loss was negatively influenced by nitrogen concentration (Fig. 4), even at relatively early stages of decomposition. Nitrogen concentrations were initially very different and increased largely in proportion to the accumulated mass loss of the litters (B. Berg, unpublished data).

The reason for suggesting nitrogen as a rate-determining factor was the fact that this could be supported by a theory including causal relationships. Two observations help to explain why mass-loss rates of the sulfuric acid lignin fraction differed among litters. Keyser et al. (1978) and Kirk et al. (1978) found that amino acids and ammonium ions repressed the formation of lignolytic enzymes in one fungal species. There now appear to be several species that have this kind of repression (P. Ander, personal communication). Provided that this finding reflects a more general phenomenon, one could expect that the higher concentrations of nitrogen in the leaves of species such as alder, may supress lignin degradation to a greater degree than the lower concentrations in brown pine needles. Another finding that may contribute to a partial explanation is that reviewed by Nömmik and Vahtras (1982). Products of lignin degradation may react with ammonia or amino acids to form recalcitrant complexes (Bremner and Shaw 1957). The results of laboratory experiments indicate that the concentration of ammonium–ammonia could be rate limiting for this kind of reaction to proceed (Axelsson and Berg 1988). Such an observation may support the present result that the lignin of the more nitrogen-rich litter had lower mass-loss rates. It is reasonable to assume that either one or both of these mechanisms may contribute to deceasing the decomposition rate of sulfuric acid lignin.

Significant negative relations were also found between the lignin-loss rate and intial concentrations of sulfur, potassium, magnesium, and calcium, of which the latter has been shown to have a rate-enhancing effect on lignin decomposition under certain pH conditions, both in laboratory cultures (Lindeberg 1944) and in a field study (Johansson 1986).

Maximum accumulated mass losses have been observed in two systems in which soil animals were either present at low levels or absent. Provided that accumulated mass losses do in fact have (species specific) upper limits at least in nutrient-poor pine systems, then a buildup of organic material should occur in at least some pine-forest systems unless fire or some other destructive agent destroys the accumulated material. This prediction is supported by observations made on islands in a north Swedish lake that have never been subjected to forest fires. These islands are almost completely covered by thick layers (2–3 m) of nondecomposed, well-aerated, organic coniferous material, in which needle structures have been found even at the bottom of the layer (O. Zachrisson, personal communication).

It should not be concluded from the present study that organic matter will also accumulate in birch and alder systems with a mull soil, at least not to the extent suggested by the maximum accumulated mass loss found here. A richer soil fauna should lead to increased fragmentation of the litter structures, thereby enhancing decomposition. Still, one cannot be certain that decomposition would be complete under such conditions.

We found significant linear relations between the maximum level for accumulated mass loss (asymptote level) and the initial phosphorus concentration, as well as the intial decomposition rate. The higher the initial phosphorus level and the initial short-term decomposition rate, the more organic material should be stored. The hypothesis supporting this includes nitrogen as an important factor, as the initial decomposition rate plays an important role for the mineralization rate of nitrogen, thereby determining the rate of release of low-molecular nitrogen compounds that can react with aromatic remains. Results from nitrogen fertilization experiments also support this. For example, in an old coniferous fertilization plot that had received about 500 kg of N·ha^{-1}·year^{-1}, Söderström et al. (1983) found that both the respiration rate and microbial counts of the humus were about 50% lower than the controls. Thus, in addition to increased growth and increased litter production, such a system that is more nitrogen rich also has a lower turnover rate of soil organic matter.

Ackowledgements

We wish to thank Annette Ewertsson for providing skilful technical assistance. Sirkka Koivuoja is gratefully acknowledged for preparing all the litter bags. Help with the computer work was provided by Birgitta Vegerfors and Hans Garmo. Two anonymous referees are gratefully acknowledged for their comments.

Axelsson, B., and Bråkenhielm, S. 1980. Investigation sites of the Swedish Coniferous Forest Project. Biological and physiographical features. Ecol. Bull. **32**: 25–64.

Axelsson, G., and Berg, B. 1988. Fixation of ammonia (^{15}N) to *Pinus silvestris* needle litter in different stages of decomposition. Scand. J. For. Res. **3**: 273–279.

Berg, B. 1991. Live fungal mycelium and lignin concentrations in some needle and leaf litter types. Scand. J. For. Res. **6**. In press.

Berg, B., and Lundmark J.-E. 1987. Decomposition of needle litter in lodgepole pine and Scots pine monocultural systems–a comparison. Scand. J. For. Res. **2**: 3–12.

Berg, B., and Staaf, H. 1980. Decomposition rate and chemical changes in decomposing needle litter of Scots pine. II. Influence of chemical composition. Ecol. Bull. **32**: 373–390.

Berg, B., and Tamm, C. O. 1991. Decomposition and nutrient dynamics of Norway spruce needle litter. I. Organic matter decomposition. Scand. J. For. Res. **6**. In press.

Berg, B., and Theander, O. 1984. The dynamics of some nitrogen fractions in decomposing Scots pine needles. Pedobiologia, **27**: 161–167.

Berg, B., and Wessen, B. 1984. Changes in organic-chemical components and ingrowth of fungal mycelium in decomposing birch leaf litter as compared to pine needles. Pedobiologia, **26**: 285–298.

Berg, B., Wessen, B., and Ekbohm, G. 1982*a*. Nitrogen level and decomposition in Scots pine needle litter. Oikos, **38**: 291–296.

Berg, B., Hannus, K., Popoff, T., and Theander, O. 1982*b*. Changes in organic-chemical components of needle litter during decomposition. Long-term decomposition in a Scots pine forest. I. Can. J. Bot. **60**: 1310–1319.

Berg, B., Ekbohm, G., and McClaugherty, C. 1984. Lignin and holocellulose relations during long-term decomposition of some forest litters. Long-term decomposition in a Scots pine forest. IV. Can. J. Bot. **62**: 2540–2550.

Berg, B., Staaf, H., and Wessen, B. 1987. Decomposition of Scots pine needle litter of differing nutrients concentrations. Scand. J. For. Res. **2**: 399–415.

Berg, B., Booltink, H. G. W., Breymeyer A., Ewertsson, A., Gallardo, A., Holm, B., Johansson, M. B., Koivuoja, S., Meentemeyer, V., Nyman, P., Olofsson, J., Pettersson, A. S., Staaf, H., Staaf, I., and Uba, L. 1991. Data on needle litter characteristics for some coniferous forest sites. 2nd ed. Sect. 2. Data on needle litter decomposition. Department of Ecology and Environmental Research, Swedish University of Agricultural Sciences, Report No. 42. In press.

Bethge, P.-O., Rådeström, R., and Theander, O. 1971. Kvantitativ kolhydratbestämning — en detaljstudie. Swedish Forest Product Research Laboratory, Stockholm, communication 63B. (In Swedish.)

Bogatyrev, L., Berg, B., and Staaf, H. 1983. Leaching of plant nutrients and total phenolic substances from some foliage litters — a laboratory study. Swedish Coniferous Forest Project Technical Report No. 33.

Bremner, J.M., and Shaw, K. 1957. The mineralization of some nitrogenous materials in soil. J. Sci. Food Agric. **8**: 341–347.

Fogel, R., and Cromack, K. 1977. Effect of habitat and substrate quality on Douglas fir litter decomposition in western Oregon. Can. J. Bot. **55**: 1632–1640.

Howard, P. J. A., and Howard, D. M. 1974. Microbial decomposition of tree and shrub leaf litter. Oikos, **25**: 311–352.

Johansson, M.-B. 1986. Decomposition rates of Scots pine needle litters in relation to site properties and litter quality. Chemical composition and decomposition pattern of leaf litters from forest trees in Sweden with special reference to methodological aspects and site properties. Swed. Univ. Agric. Sci. Rep. For. Ecol. For. Soils No. 56.

Keyser, P., Kirk, T. K., and Zeikus, I. G. 1978. Ligninolytic enzyme of *Phanerochaete chrysosporium*: synthesized in absence of lignin in respone to nitrogen starvation. J. Bacteriol. **135**: 790–797.

Kirk, T. U., Schultz, E., Connors, W. I., Lorbaz, L. F., and Brauns, I. G. 1978. Influence of culture parameters on lignin metabolism by *Phanerochaete chrysosporium*. Arch. Microbiol. **117**: 227–285.

Lindeberg, G. 1944. Uber die Physiologie Ligninabbauender Bodenhymenomyzeten. Symb. Bot. Ups. **8** (2). (In German, English summary.)

McClaugherty, C., and Berg, B. 1987. Cellulose, lignin and nitrogen levels as rate regulating factors in forest litter decomposition. Pedobiologia, **30**: 101–112.

Melin, E. 1930. Biological decomposition of some types of litter from North American forests. Ecology, **11**: 72–101.

Millar, H. C., Smith, F. B., and Brown, P. E. 1948. The rate of decomposition of various plant materials in soils. J. Am. Soc. Agron. **28**: 914–923.

Nömmik, H., and Vahtras, K. 1982. Retention and fixation of ammonium and ammonia in soils. *In* Nitrogen in agricultural soils. *Edited by* F. J. Stevenson. Agronomy Monographs, No. 22, Agronomy Society of America, Madison, WI. pp. 123–171.

Norden, B., and Berg, B. 1989. A non-destructive method (solid state ^{13}C-NMR) to determine organic-chemical components in decomposing litter. Soil Biol. Biochem. **19**: 589–593.

Persson, T., Bååth, E., Clarholm, M., Lundkvist, H., Söderström, B., and Sohlenius, B. 1980. Trophic structure, biomass dynamics and carbon metabolism of soil organisms in a Scots pine forest. Ecol. Bull. **32**: 419–462.

SAS Institute Inc. 1979. SAS user's guide. SAS Institute, Inc., Sparks Press, Raleigh, NC.

Staaf, H., and Berg, B. 1982. Accumulation and release of plant nutrients in decomposing Scots pine needle litter. Long-term decomposition in a Scots pine forest II. Can. J. Bot. **60**: 1561–1568.

Appendix

Table A1. Linear relations for lignin mass loss vs. time for seven litter types incubated in a 130-year-old Scots pine forest

Litter type	Equation	R^2	*n*
White birch, brown leaves	$y = 2.96 + 0.02199x$	0.845	13
White birch, green leaves	$y = 3.41 + 0.0312x$	0.949	13
Scots pine, brown needles	$y = 7.27 + 0.0373x$	0.960	11
Scots pine, green needles	$y = 0.0280 + 0.0353x$	0.984	11
Lodgepole pine, brown needles	$y = 0.240 + 0.0418x$	0.953	13
Lodgepole pine, green needles	$y = 6.93 + 0.0390x$	0.954	12
Grey alder leaves	$y = 4.933 + 0.0197x$	0.918	12

Note: Data on mass loss and concentrations of lignin and nitrogen in tissue at each sample time can be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council of Canada, Ottawa, Ont., Canada K1A 0S2.